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Impact of deforestation on habitat connectivity thresholds for large carnivores in tropical forests

Miriam A. Zemanova[1,2], Humberto L. Perotto-Baldivieso[3,4*], Emily L. Dickins[5], Andrew B. Gill[1,6], John P. Leonard[3] and David B. Wester[3]

Abstract

Introduction: Deforestation significantly impacts large carnivores that depend on large tracts of interconnected forest habitat and that are sensitive to human activities. Understanding the relationship between habitat use and spatial distribution of such species across human modified landscapes is critical when planning effective conservation strategies. This study assessed the presence of potential landscape connectivity thresholds resulting from habitat fragmentation associated with different deforestation patterns using a scale-based approach that links species-specific home ranges with the extent of anthropogenic activities. The objectives were (1) to quantify the spatial and temporal distribution of natural vegetation for five common deforestation patterns and (2) to evaluate the connectivity associated with these patterns and the existence of potential thresholds affecting jaguar dispersal. The Bolivian lowlands, located within jaguar conservation units, were analysed with landscape metrics to capture the spatial and temporal changes within deforested areas and to determine potential impact on jaguar connectivity and connectivity thresholds for dispersal.

Results: Over the period of 1976–2005, the amount of natural vegetation has decreased by more than 40% in all locations with the biggest changes occurring between 1991 and 2000. Landscape spatial structure around jaguar locations showed that jaguars used areas with mean proportion of natural areas = 83.14% (SE = 3.72%), mean patch density = 1.16 patches/100 ha (SE = 0.28 patches/100 ha), mean patch area = 616.95 ha (SE = 172.89 ha) and mean edge density = 705.27 m/ha (SE = 182.19 m/ha).We observed strong fragmentation processes in all study locations, which has resulted in the connectivity of jaguar habitat decreasing to <20% by 2005. A connectivity threshold zone was observed when the proportion of natural vegetation was less than 58.4% (SE = 1.3).

Conclusions: Assessing fragmentation and connectivity for carnivores within the extent of human-modified landscapes proved to be an effective way to understand the changes caused by deforestation and their potential effects on large carnivore habitats. Our study highlights the importance of scale-based approaches for assessing current conservation challenges to protect large carnivores.

Keywords: Bolivian lowlands, Habitat fragmentation, Landscape metrics, *Panthera onca*, Threshold

* Correspondence: humberto.perotto@tamuk.edu
[3]Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Blvd. MSC 218, Kingsville, TX 78363, USA
[4]Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel Rene Moreno, Avenida Irala 565, Santa Cruz de la Sierra, Bolivia
Full list of author information is available at the end of the article

Zemanova *et al. Ecological Processes* (2017) 6:21

Page 2 of 11

Introduction

Pressures, such as population growth and socio-economic improvements to human welfare, have significantly increased demands for agricultural goods and services (Rudel and Roper 1997; Lorena and Lambin 2009; Ziolkowska et al. 2012). Increased deforestation rates across the world in particular have had profound consequences for species composition and distribution (Zipperer 1993). The impacts of deforestation have been widely documented through changes in the spatial configuration and habitat quality of remaining habitat fragments, biophysical functions of the landscape, fauna and flora composition and loss of natural habitat (e. g. Steininger et al. 2001a; Steininger et al. 2001b; Dixo et al. 2009; Scolozzi and Geneletti 2012). One of the consequences of deforestation and a major challenge in conservation biology is habitat fragmentation (Zipperer 1993; Dixo et al. 2009; Rueda et al. 2013). In recent years, it has become increasingly important to better understand the ecological consequences of fragmentation due to the expansion and intensification of land use (Baggio et al. 2011; Ziolkowska et al. 2012).

Fragmentation by deforestation occurs through the loss of natural habitat and the pattern of clearing, which result from the interactions of biotic, abiotic and human socio-political factors (Zeilhofer et al. 2014). Fragmentation has a significant effect on overall habitat availability and quality (Dixo et al. 2009) with consequences for species survival, abundance, dispersal and the functional linkages amongst habitat patches (Scolozzi and Geneletti 2012; Gao et al. 2013). Different fragmentation patterns (i.e. geometric, corridor, fishbone, diffuse, radial and island) caused by deforestation have contributed to different species survival and dispersal rates (Geist and Lambin 2001; Millington et al. 2003; Lorena and Lambin 2009) and can limit species' ability to colonise an area by imposing an isolation barrier (Kindlmann and Burel 2008). Geist and Lambin (2001) and Lorena and Lambin (2009) provide detailed descriptions of abovementioned deforestation patterns. These landscape changes are particularly important for large carnivores because they depend on large tracts of undisturbed habitat and are highly sensitive to human activities, such as habitat loss and degradation, prey depletion by local communities hunting and perceived threats to those communities and their domestic species (Jackson et al. 2005; Cavalcanti and Gese 2009, 2010; Horev et al. 2012; Zeilhofer et al. 2014). Fragmentation also affects the gene flow within declining populations and hence increases extinction risk (Vandermeer and Lin 2008; Zeilhofer et al. 2014; Roques et al. 2016). Therefore, understanding the loss of connectivity that can affect the dispersal ability and movement patterns of large carnivores across fragmented landscapes is critical for implementing conservation strategies (Pascual-Hortal and Saura 2006; Vogt et al. 2009).

Landscape connectivity, defined as the degree to which a landscape facilitates or impedes movement of a species (Taylor et al. 1993), is critical because of its direct impact on the maintenance of ecological function and population persistence and survival of a species (Pascual-Hortal and Saura 2006; Kool et al. 2013). The use of graph theory has proven valuable in addressing structural connectivity measures across different scales and has been shown to be a robust methodology to assess patch and landscape connectivity (Saura and Pascual-Hortal 2007; Scolozzi and Geneletti 2012). Quantifying structural connectivity is species-specific and requires relevant behaviour and dispersal information to define spatial and temporal scales for connectivity assessment (Dixo et al. 2009; Perotto-Baldivieso et al. 2009; Kool et al. 2013). Addressing fragmentation and structural connectivity by integrating the scales at which deforestation processes and wildlife dispersal operate can significantly contribute to a new conservation paradigm (i.e. incorporation of human modified landscapes in conservation strategies for species dispersal) proposed by Chazdon et al. (2009). Furthermore, scale-based approaches can represent a solution to scale mismatches that have resulted in failure to achieve conservation objectives (Delsink et al. 2013).

Assessing species dispersal within the extent of human activities that cause landscape fragmentation can provide an indication of critical thresholds at which a species can be significantly impacted by fragmentation (Oliveira de Filho and Metzger 2006). Whilst there is evidence that these thresholds are important to identify breakpoints where species dispersal significantly changes owing to loss of habitat, there is growing consensus that there is not a single 'fragmentation threshold' applicable across species because of significant variability in the response of wildlife to habitat structural changes (Swift and Hannon 2010; Martensen et al. 2012). Specific ecological thresholds should be identified for individual species (Johnson 2013). To date, it has been difficult to integrate processes operating at different scales, such as deforestation and species movement, to successfully achieve conservation objectives (Delsink et al. 2013). It is critical to determine whether there are minimum amounts of natural vegetation that may limit species dispersal across these modified landscape patterns.

The tropical lowlands of Bolivia have been affected considerably by anthropogenic activities in the last three decades (Killeen et al. 2007). Agricultural subsistence colonisation (1970s), spontaneous colonisation (1980s) and industrial agriculture initiatives (1990s) have significantly increased deforestation in the country (Steininger et al. 2001b; Millington et al. 2003; Killeen et al. 2007; Killeen et al. 2008; Arancibia Arce et al. 2013). These events have generated distinctive deforestation patterns (e.g. geometric, diffuse, fishbone, radial) across areas

Zemanova *et al. Ecological Processes* (2017) 6:21

Page 3 of 11

(Geist and Lambin 2001; Steininger et al. 2001a; Mertens et al. 2004) with significant impacts on natural vegetation. These areas have also been identified as critical for the dispersal of jaguars (*Panthera onca*) in their southern distribution range (Sanderson et al. 2002; Rabinowitz and Zeller 2010). The jaguar is an appropriate choice for this study because of its broad but declining distribution and its value as a flagship species across the Americas (Sanderson et al. 2002; Cavalcanti and Gese 2010; Rabinowitz and Zeller 2010; Tobler et al. 2013). Jaguars are an excellent example of a large ranging predator that depends on undisturbed habitat for movement across a variety of ecosystems (Baggio et al. 2011). They are also very sensitive to human presence and human activities (De Angelo et al. 2013). Where human activities focus on livestock production, jaguars could shift their behaviour towards prey preferences from wildlife species to domestic livestock (Cavalcanti and Gese 2009, 2010). On the other hand, where human activities focus on farming, there is a potential for natural prey loss and habitat degradation (Zeilhofer et al. 2014). In both cases, habitat loss and potential persecution by local farmers and ranchers significantly affect population persistence (Petracca et al. 2014).

Therefore, the aim of this study was to assess the presence of potential structural connectivity thresholds due to fragmentation in different deforestation patterns with a scale-based approach that links species-specific home ranges with the extent of anthropogenic activities. The objectives were (1) to quantify the spatial and temporal distribution of natural vegetation for five common deforestation patterns over three decades and (2) to evaluate the degree of connectivity and the existence of potential thresholds that could affect jaguar dispersal. We hypothesised that the deforestation patterns identified in our study area would be reflected in significantly different habitat fragmentation and structural connectivity for jaguars until a threshold zone between the proportion of natural vegetation and connectivity is reached.
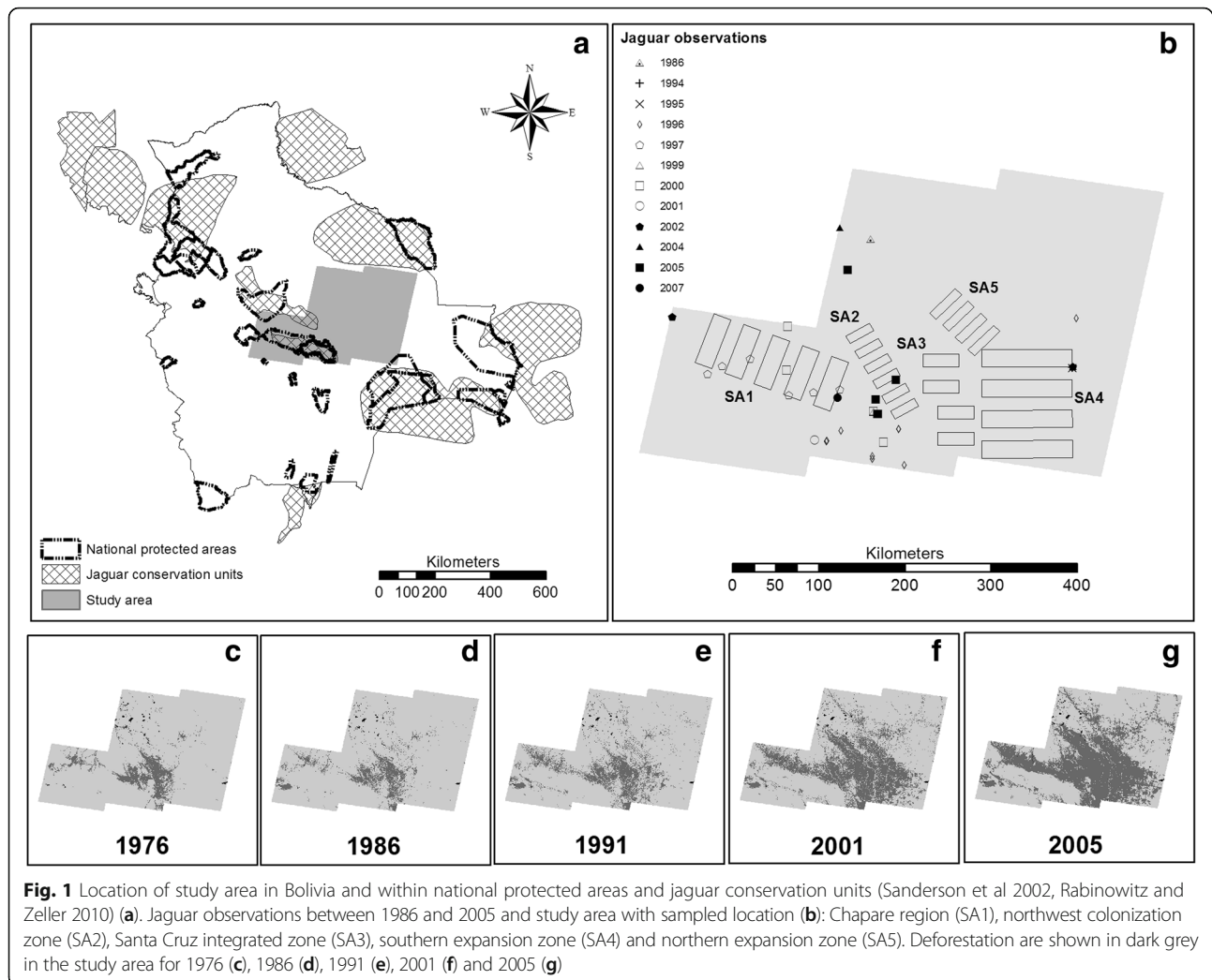
Methods

Study area

The study site was located in the Bolivian lowlands and foothills East of the Andes (Fig. 1a) where large-scale deforestation driven by agricultural activities has taken place in the last three decades (Fig. 1c–g) (Killeen et al. 2007, 2008). This area is located at the centre of areas identified with good potential for jaguar conservation (known as jaguar conservation unit (JCU)) (Fig. 1a) proposed initially by Sanderson et al. (2002) and further developed by Rabinowitz and Zeller (2010). The five study locations (SA) were selected according to the deforestation pattern and socio-economic situation identified in

the Bolivian lowlands (Fig. 1b). Deforestation patterns were described using the typology of Geist and Lambin (2001):

- The Chapare region (SA1; pre-Andean and lowland Amazon forests, most humid) is driven mainly by small scale subsistence and commercial agriculture, coca (*Erythroxylum coca*) production and timber harvesting (Millington et al. 2003; Bradley and Millington 2008). Crops are mostly perennials grown extensively (Superintendencia Agraria 2001). Deforestation has been undertaken in fishbone patterns expanding out from main and secondary roads. The Chapare region is recognised for its importance to biodiversity, and it is surrounded by three National Parks in the area: Carrasco, Amboró and Isiboro Sécure.

- The northwestern colonization zone (SA2; lowland humid and semi-deciduous, Amazon and Chiquitano forests) is one of the oldest and most successful small-scale farming schemes (Mertens et al. 2004). This area was colonized by directed migrations, causing a diffuse pattern initially which later coalesced into a more geometric pattern of intensified deforestation, with most deforestation (~80%) occurring before 1995. Currently most of the land use conflicts occur between timber companies, forest reserves (el Chore forest reserve) and spontaneous migrations into the area.

- The Santa Cruz integrated zone (SA3; lowland Chiquitano semi-deciduous forest) is inhabited by Cruceño farmers (Cruceño refers to the people from Santa Cruz Department), Japanese and Mennonite farmers. This area is known to be the traditional centre of large-scale agriculture in the Bolivian lowlands (Mertens et al. 2004). This region was one of the first areas to be subject to large-scale deforestation with geometric patterns mostly occurring before 1980. Crops in this area are grown on rotation combined with improved and natural pastures. This area has one of the most developed road infrastructures in the lowlands with a very high road density.

- The southern expansion zone (SA4; lowland Chiquitano and Chaco dry forests) lies east of the Rio Grande River. The mechanised farming sector has grown steadily (Vanclay et al. 1999), managed mainly by large agro-industrial corporations. Intensive rotational cropping systems dominate the agricultural activities in the area. This has resulted in large-scale farmers clearing very large blocks of land, mostly eastwards of the Santa Cruz integrated zone (SA3) following large geometric patterns. The national protected area, Kaa-Iya del

Fig. 1 Location of study area in Bolivia and within national protected areas and jaguar conservation units (Sanderson et al 2002, Rabinowitz and Zeller 2010) (**a**). Jaguar observations between 1986 and 2005 and study area with sampled location (**b**): Chapare region (SA1), northwest colonization zone (SA2), Santa Cruz integrated zone (SA3), southern expansion zone (SA4) and northern expansion zone (SA5). Deforestation are shown in dark grey in the study area for 1976 (**c**), 1986 (**d**), 1991 (**e**), 2001 (**f**) and 2005 (**g**)

Gran Chaco National Park lies to the southeast of this area.

- The northern expansion zone (SA5; lowland humid Chiquitano forest) originated from the San Julián resettlement scheme of indigenous people from the Andes where small nucleated settlements lie central to soybean agricultural fields extending out in radial patterns (Steininger et al. 2001a). Crops are grown in extensive rotations. Classic fishbone patterns along the secondary roads, combined with island deforestation patterns from small settlements, are removing natural vegetation composed of deciduous and semi-deciduous forests (Mertens et al. 2004).

Data collection and analyses

To facilitate the understanding of deforestation patterns and fragmentation that affect jaguars across a variety of habitats, we focused on the natural and anthropogenic changes between 1976 and 2005. The land-cover change database published by Killeen et al. (2007) was reclassified in ArcGIS (ESRI; Redlands, CA) into three categories: natural, anthropogenic and water. This database represents the land-cover in the study area in years 1976 (Fig. 1c), 1986 (Fig. 1d), 1991 (Fig. 1e), 2001 (Fig. 1f) and 2005 (Fig. 1g). The details on the original land cover classes, satellite platform (LANDSAT program), spatial resolution (30 m) and the classification methodology for the land-cover change database are described in Killeen et al. (2007). Two scales were used for our analyses: the scale or extent of human activity and within this scale, the extent of female jaguar home ranges reported by Maffei et al. (2004). For each study location (SA1–SA5), spatial sampling captured the extent of the deforestation process caused by human activities and its variability within study locations. Using the 2005 land-cover database map (Killeen et al. 2007), evenly separated rectangular blocks were delineated perpendicular to the main road associated with deforestation. The length was defined by the extent of continuous deforestation for each SA (Fig. 1b). Therefore, the size of each sampling block was different for each

location (Table 1), but each sampling block was separated by 10 km to reduce spatial and/or temporal autocorrelation (Odland 1988; Minta 1992). Spatial autocorrelation refers to the degree of similarity between observations recorded at points that are close to each other in space and/or time. Minimizing autocorrelation provides independent data for valid statistical analyses (Perotto-Baldivieso et al. 2012a). The 10 km distance was chosen because it represents at least three times the mean diameter for jaguar home ranges reported by Maffei et al. (2004). For each block and for each time period, fragmentation was quantified with the landscape metrics: percentage of natural vegetation cover (%; PLAND), mean patch size (ha), patch density (patches/100 ha) and edge density (m/ha) (Millington et al. 2003; Perotto-Baldivieso et al. 2011; McGarigal et al. 2012; Zeilhofer et al. 2014). Mean and standard errors for each metric were calculated for each location and time period between 1976 and 2005.

Connectivity was assessed for each sampling block and time period using the integral index of connectivity (IIC) (Pascual-Hortal and Saura 2006). This metric is a graph-based index employed to assess connectivity using graph theory (Neel 2008; Perotto-Baldivieso et al. 2009; Visconti and Elkin 2009) and it was calculated using Conefor Sensinode 2.6 (Saura and Torne 2009). Connectivity values can range from zero to one, with one being the highest connectivity value. To understand the impact of fragmentation on jaguar habitat connectivity within each block, a distance threshold of 3 km was used between connecting patches. This distance corresponds to the radius of an average home range of 29 km^2 reported for female jaguars in continuous dry forest habitats in the eastern regions of Bolivia (Maffei et al. 2004), the closest home range observation in the region.

The relationship between PLAND and IIC was analysed with linear and nonlinear regression models using the results from the sampling blocks and time periods (Table 1). A straight-line relationship between connectivity and natural vegetation would indicate that the estimated change in connectivity with a unit change in natural vegetation is constant across the range of natural vegetation, which in turn suggests that there is no breakpoint in natural vegetation with respect to corresponding changes in connectivity (Gujarati and Porter 2009). In contrast, a curvilinear relationship between connectivity and natural vegetation, which can be estimated with a number of

models (e.g. multiple linear polynomial models, simple nonlinear exponential model) would suggest the presence of a breakpoint (or region) where connectivity changes in a different way to changes in natural vegetation which can be useful for applications in conservation and management strategies. Because we lacked replicated values of connectivity for given values of natural vegetation, a formal test of lack-of-fit of a simple linear model (Kutner et al. 2004) was not possible. However, presence of a significant quadratic term in a polynomial model indicates that a curvilinear relationship is a better fit than a simple linear model (Kendall and Stuart 1966). We used PROC REG in SAS 9.3 (SAS Institute INC.; Cary, NC) to estimate connectivity as a function of natural vegetation in simple linear and quadratic polynomial models in PLAND; PROC NLIN in SAS 9.3 (SAS Institute INC.; Cary, NC) was used for a simple nonlinear exponential model. Because both polynomial and exponential models were a better fit than a simple linear model, we concluded that there was a curvilinear relationship between connectivity and natural vegetation, and so, we estimated a breakpoint using Davies test (Davies 1987; Muggeo 2003; Muggeo 2008) and piecewise linear regression methods (Gujarati and Porter 2009) both of which provide standard errors of estimated breakpoints. We used the estimated breakpoint from Davies test as the starting point in PROC NLIN for the parameter search for C in the model l.

$$\text{IIC} = \beta_0 + \beta_1 \text{PLAND} + \beta_2 (\text{PLAND} - C)D + \epsilon_i$$

(1)

where C is estimated breakpoint and D is dummy variable equal to 0 when $PLAND < C$ and 1 when $PLAND \geq C$. Analysing Eq. 1 with a multiple linear regression analysis (PROC REG, SAS 9.3, Cary, NC) with the independent variable ($PLAND - C$) yielded similar results for breakpoint values in the piecewise linear regression method and Davies test.

Additionally, available jaguar observation data (capture data, sightings, faecal samples, footprints) collected between 1985 and 2007 located in the study area were acquired from Lopez-Strauss et al. (2010) and downloaded from the Geospatial Centre for Biodiversity (www.museonoelkempff.org/cgb; Perotto-Baldivieso et al. 2012b) to quantify the landscape spatial structure around areas where these observation data were recorded. A total of 777 jaguar observation records (680 records from Lopez-Strauss et al. (2010), and 97 records from Geospatial Centre for Biodiversity) were publicly available for the entire country. From this database, only 63 records were located within our study area and 39 records (one record 1986, one record 1994, one record 1995, 14 records 1996, six records 1997, one record 1999, four records 2000, one record 2001, two records 2002, two records

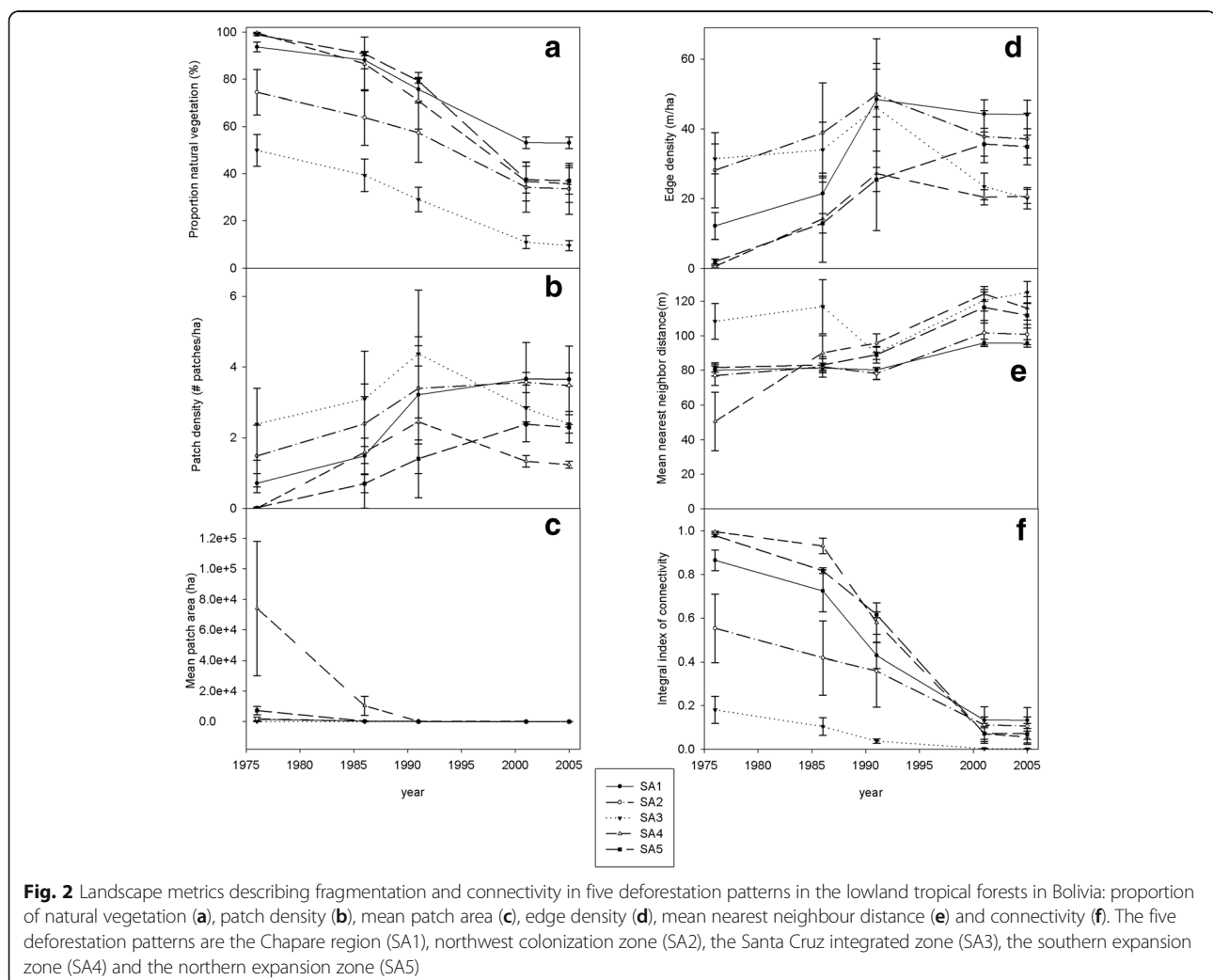**Table 1** Sampling design for the five deforestation patterns

Study area	SA1	SA2	SA3	SA4	SA5
Number of transects	5	6	4	4	4
Dimensions (km)	60 × 20	30 × 10	40 × 15	100 × 20	40 × 10
Area (km^2)	1200	300	600	2000	400
Spacing (km)	15	10	15	15	10

Zemanova *et al. Ecological Processes* (2017) 6:21

Page 6 of 11

2004, five records 2005, one record 2007) were used. The remaining 24 observation records had to be excluded due to the lack of information regarding the year of observation (15 records) or potential record redundancy (three records had same coordinates and same year in three different locations: nine records total). The purpose of this analysis was to quantify the spatial structure of natural vegetation that was potentially used by jaguars based on published and verified observations within the study area. For each of the used jaguar observations, a circular buffer area representing a 29 km^2 home range was simulated and the same landscape metrics from our spatial modelling (i.e. PLAND, mean patch size, patch density and edge density) were calculated using FRAGSTATS 4.2 (McGarigal et al. 2012). Mean values and standard errors were calculated for these metrics.

Results

Over the period of 1976–2005, PLAND decreased in all locations with the biggest changes occurring between 1991 and 2000. The areas most affected by these changes were the expansion zones SA4 (geometric deforestation patterns) and SA5 (radial deforestation patterns) where the percentage of natural vegetation decreased from 71 to 79%, respectively, in the 1990s to 37% in 2001 (SA4 and SA5) (Fig. 2a). The high variability in the proportion of natural vegetation (Fig. 2a) indicates that deforestation processes were occurring at different rates within locations. Patch density increased between 1976 and 2005 in all locations (Fig. 2b), with reduction in mean patch area (Fig. 2c) and increase in edge density (Fig. 2d). Hence, fragmentation process occurred in all locations, with the highest rates observed in the expansion zones SA4 and SA5 followed by the newly colonised zones SA1 (fishbone deforestation pattern) and SA2 (diffuse deforestation pattern). Patch density (Fig. 2b) and edge density (Fig. 2d) values increased throughout the study period in SA1, SA2 and SA5, whereas peak values were observed in 1991 for SA3 (geometric deforestation patterns) and SA4. Mean nearest

Fig. 2 Landscape metrics describing fragmentation and connectivity in five deforestation patterns in the lowland tropical forests in Bolivia: proportion of natural vegetation (**a**), patch density (**b**), mean patch area (**c**), edge density (**d**), mean nearest neighbour distance (**e**) and connectivity (**f**). The five deforestation patterns are the Chapare region (SA1), northwest colonization zone (SA2), the Santa Cruz integrated zone (SA3), the southern expansion zone (SA4) and the northern expansion zone (SA5)

Zemanova *et al. Ecological Processes* (2017) 6:21

Page 7 of 11

neighbour distances increased (Fig. 2e), and IIC decreased in all locations with values at their lowest (<0.2) after 2001 (Fig. 2f). Lowest IIC values were observed in SA2 and SA3. The highest declines in IIC were observed in the expansion zones SA4 and SA5 where agriculture increased significantly after the 1990s.

Although PLAND explained 88% of the variation in IIC in a simple linear model, a significant partial quadratic term ($F_{1110} = 810$, $P < 0.0001$) in a multiple linear model indicated that IIC changed in a nonlinear fashion with changes in PLAND. A nonlinear model ($r^2 = 0.989$; $P < 0.0001$) and a piecewise linear model ($r^2 = 0.985$; $P < 0.0001$; EQ. 3; Fig. 3) had coefficients of determination that exceeded 98%. Breakpoint values from Davies test (PLAND = 58.4; SE = 1.3; $P < 0.0001$) and piecewise linear regression (PLAND = 58.4; SE = 1.2; $P < 0.0001$) are very similar (Fig. 3). The piecewise linear regression showed that when PLAND cover was less than ~58%, connectivity increased 0.0036 (SE = 0.0003) units for each percent increase in PLAND; in contrast, when PLAND cover was greater than ~58%, connectivity increased 0.0161 (SE = 0.0006) units for each PLAND cover (Fig. 3). These two rates of change differed significantly below and above the breakpoint value ($F_{1110} = 192$, $P < 0.0001$).

Landscape spatial structure around jaguar observation data showed that jaguars used areas with mean PLAND = 83.14% (SE = 3.72%), mean patch density = 1.16 patches/100 ha (SE = 0.28 patches/100 ha), mean patch area = 616.95 ha (SE = 172.89 ha) and mean edge density = 705.27 m/ha (SE = 182.19 m/ha).

Discussion

Scale-based approaches are central to understanding the variability in the changes caused by deforestation and their potential effects on large carnivores' habitat. Our study focused on assessing fragmentation and natural vegetation structural connectivity applying the spatial scale of habitat used by jaguars within the extent of human-modified landscapes. Our results showed that after 2001, areas with <58% (SE = 1.3) PLAND had a reduction of more than 80% in IIC values (i.e. connectivity) which may be a strong factor affecting jaguar abundance in the region. The results from the landscape spatial structure analysis based on jaguar observation data indicate that jaguars used areas with PLAND around 83% and with little fragmentation. The comparison of jaguar observation data landscape metrics with those from the sampling blocks after 2001 (Fig. 2) indicates that there may no longer be adequate natural vegetation to support resident female jaguars. The loss of natural vegetation has serious negative impacts on jaguar populations, but responses can be complex and could be exacerbated by further anthropogenic intervention on the landscape

over long periods of time (De Angelo et al. 2013; Tobler et al. 2013; Kosydar et al. 2014). Fragmentation can cause a loss in connectivity with negative effects on food resources, female and/or male home ranges, flow of genetic material, subpopulations persistence and the probability of extinction risk (Saura and Pascual-Hortal 2007; Cavalcanti and Gese 2009; Reding et al. 2013). Losses in structural connectivity can also lead to losses in functional connectivity. As large patches of natural vegetation decrease, habitat for jaguar preys also decrease. Zimbres et al. (2017) showed that terrestrial mammal diversity depends on large tracts of natural vegetation along riparian corridors. Therefore, fragmentation due to agricultural activities would decrease jaguar habitat, prey habitat, and ecological function, thus limiting cover and food resources across the landscape. This also may increase the chances of human-wildlife encounter making jaguars more vulnerable to human activity and human intervention (Petracca et al. 2014; Olsoy et al 2016). Human expansion in our study areas will compete with jaguars for the availability of food resources through hunting and increase the potential for human-wildlife conflicts in ranching areas (Rumiz et al. 2012). Petracca et al. (2014) reported that 65% of people had negative attitudes and fear towards jaguars. Given this scenario, one important question to answer is how much deforestation can happen before jaguar population persistence is lost.

Our study revealed that once landscapes have <58.4% natural vegetation (SE = 1.3), structural connectivity within jaguar home ranges was lower than 20%. When PLAND was less than ~58%, connectivity only increased by 0.0036 units for each percent increase in PLAND while above ~58%, it increased by 0.0161 units (Fig. 3). This breakpoint value (and its standard error) in the relationship between PLAND and IIC could be interpreted as a threshold zone by which landscape permeability based on jaguar dispersal distances within the home range area may have been lost. Thresholds remain controversial, but there is evidence in theoretical and empirical studies that habitat loss has a significant effect on species occurrence within landscapes (Martensen et al. 2012; Johnson 2013). The existence of a threshold zone in structural connectivity may imply changes in natural vegetation dynamics, decreased availability of food resources, increased contact with humans and potentially human-jaguar conflicts (Altrichter et al. 2006; Rumiz et al. 2012; Young et al. 2014). Although jaguars may move across fragmented landscapes, they tend not to use small patches (<200 ha) as they prefer natural vegetation patches > 2000 ha (Ramirez-Reyes et al. 2016). In our study, we did not find mean patch sizes greater than 30 ha (±10.01) after 2001. This suggests that viable jaguar habitat may be very limited in the lowlands and foothills East of the Andes.
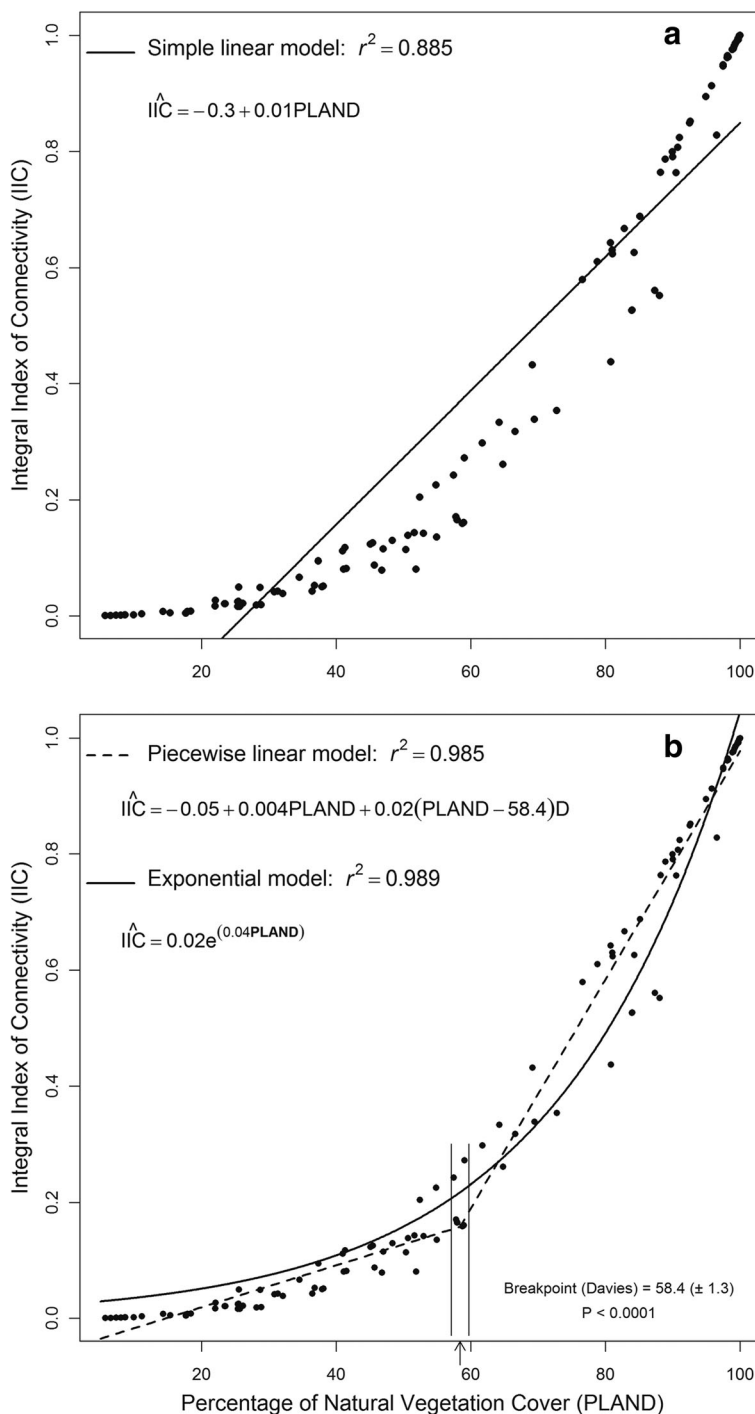
Fig. 3 Relationship between the percentage of natural vegetation (PLAND) and integral index of connectivity (IIC). Straight line represents the estimated regression equation based on a simple linear model (**a**). The *dashed lines* represent a piecewise linear regression model (where $C = 58.4$ is the threshold point and D is a dummy variable with $D = 0$ for $C < 58.4$ and $D = 1$ for $C \geq 1$), and the *vertical arrows* represents the breakpoints identified using the Davies test (with ± se) (**b**)

The significant loss of natural vegetation has potential implications not only at local scales but also at regional scales. Our study area is located at the centre of JCUs (Sanderson et al. 2002; Rabinowitz and Zeller 2010) and connects the jaguar populations of the Pantanal, the Chacoan region, the Eastern Andes, and the Amazon (Fig. 1a). Although there are several protected areas currently overlapping with JCUs (Fig. 1a), the land-cover

Zemanova *et al. Ecological Processes* (2017) 6:21

Page 9 of 11

changes reported in our study area are already likely to have caused a significant decline in connectivity over the past few decades. Given the amount of deforestation observed in the study area, it seems unlikely that conservation strategies that aim at increasing core habitat areas and/or maintaining structural connectivity will be effective in similar lowland tropical forests to maintain connectivity for large carnivore populations. Significant conservation efforts will be necessary to integrate habitat restoration and land management strategies that can significantly reduce or reverse current deforestation trends in these areas. Ecological threshold zones, such as the natural breakpoint observed in IIC and PLAND could potentially be used for conservation and management strategies to distinguish habitat management and conservation zones (areas above ecological thresholds), from areas where restoration will be needed (areas below ecological thresholds). Based on the land-cover database published by Killeen et al. (2007), our results show that loss of vegetation was greatest between 1991 and 2001. These changes have had greater significance during this time period due to social (e.g. large Andean migrations to the lowlands) and economic factors (e.g. soybean production, cattle ranching) that affected the country at a national scale (Killeen et al. 2007, 2008; Arancibia Arce et al. 2013). This is consistent with economic and social trends reported for our study area (Kaimowitz et al. 1999; Steininger et al. 2001a; Pacheco 2002; Killeen et al. 2008). Unfortunately, the trend has continued in the last decade with reported deforestation rates as high as 200,000 ha/year (Müller et al. 2014; Tejada et al. 2016) which is exacerbating poor habitat availability for wildlife in the lowland areas of Bolivia even more.

Conclusions

Although jaguars use a variety of habitats, land use change, habitat fragmentation and degradation can significantly affect their population persistence (Cavalcanti and Gese 2009). The impact of agriculture and the recent surge of gold mining in the Amazon (Tobler et al. 2013) are likely to exacerbate the reduction in vegetation extent with long-term impacts on jaguar population. This may be compounded by hunting and other potential human-jaguar conflicts (Altrichter et al. 2006; Rumiz et al. 2012). The effects of deforestation and loss of natural habitat are affecting a large number of species around the world. The use of relevant scales, that is the extent of human activity and their impact on species dispersal and home range, can be applied to a number of other species across the world where loss of natural habitat is affecting population abundance and survival. Our results also underscore the importance of providing scale-based approaches for assessing current conservation challenges to protect large carnivores and other species around the world.

Authors' contributions
MAZ and HLP made substantial contributions to conception, design, and acquisition of data. All authors provided significant contributions to the analysis and interpretation of the data, and they have been involved in drafting the manuscript and revising it critically for important intellectual content. MAZ, HLP, ELD, ABG, JPL, and DBW have given final approval of the version to be published; they take public responsibility for appropriate portions of the content; and they have agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

Competing interests
The authors declare that they have no competing interests.

Consent for publication
Not applicable.

Ethics approval and consent to participate
Not applicable.

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Author details
[1]School of Energy, Environment and Agrifood, Cranfield University, Cranfield MK43 0AL, UK. [2]Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland. [3]Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, 700 University Blvd. MSC 218, Kingsville, TX 78363, USA. [4]Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel Rene Moreno, Avenida Irala 565, Santa Cruz de la Sierra, Bolivia. [5]Hensmans Farm, Nearton End, Swanbourne MK17 0SL, UK. [6]Cape Eleuthera Institute, Eleuthera, Bahamas.

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Page 10 of 11

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Page 11 of 11

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